A REVIEW OF THE PARDALIS-MACULATUS COMPLEX OF THE BOID GENUS TROPIDOPHIS OF THE WEST INDIES

By Albert Schwartz and Robert J. Marsh

No. 2 *A review of the* PARDALIS-MACULATUS *complex of the boid genus* TROPIDOPHIS *of the West Indies.*

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The small, multispotted boas of the genus *Tropidophis*, in the West Indies, have proven a troublesome group to many American workers concerned with West Indian herpetology. This is especially true if one is interested in Cuban reptiles, since the complex is represented there by several forms. On Cuba, as well, occur representatives of two other major groups of the genus, the larger, and keeled-scaled *T. melanurus* and the prominently and contrastingly spotted group consisting of *T. semicinctus, T. wrighti* and *T. feicki* (Schwartz, 1957). In the present paper we will attempt to clarify the relationships in the nominal species *T. pardalis* and *T. maculatus*, as well as those of *T. nigriventris*. The situation appears to be far more complicated than has been previously considered, and it has only been through the assembling of much material that the present conclusions have been reached.

The only attempt to revise the genus *Tropidophis* is that of Stull (1928). At the time of this revision, there were 177 specimens of the genus in collections in the United States; these specimens represented eleven of the thirteen forms which Miss Stull regarded as valid. These thirteen forms were divided by her into two major groups: 1) the *maculatus* group (including the named forms *maculatus, jamaicensis, haetianus*, and *paucisquamis*) characterized by smooth scales, bifurcate and longitudinally laminate hemipenes; and 2) the *pardalis* group (*taczanowskyi pardalis, canus, curtus, androsi, bucculentus, wrighti, melanurus,* and *semicinctus*) characterized by more or less keeled scales, and a quadrifurcate hemipenis which is longitudinally flounced in the secondary forks and transversely flounced in the primary forks. Of these named forms, we have concerned ourselves with the South American *taczanowskyi* and *paucisquamis* only briefly and not at all with the distinct *melanurus* (and its Cayman subspecies *parkeri* and *caymanensis;* see Grant, 1941a), nor the *semicinctus* complex as noted above. The snake regarded as *T. pardalis bucculentus* by Miss Stull is considered by us as more closely related to *T. melanurus*, as Bailey (1937 :45) has pointed out, and thus not within the province of the present paper.

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Since the publication of Miss Stull's revision, several other snakes belonging to the complex under study have been described. In 1936, Barbour and Shreve described *T. pardalis greenwayi* on the basis of two specimens from Ambergris Cay, Caicos Islands, in the Bahamas. Bailey (*op. cit.*) later described *T. nigriventris* and *T. maculatus pilsbryi* from limited material from Cuba and *T. pardalis barbouri* from several islands in the Bahamas; finally, in 1940, Grant described two new forms from Jamaica, *T. pardalis stejnegeri* and *T. maculatus stulli*. The named forms which we will consider in this paper thus include the following:

Tropidophis pardalis pardalis Gundlach, 1840
Tropidophis pardalis canus Cope, 1868
Tropidophis pardalis curtus Garman, 1887
Tropidophis pardalis androsi Stull, 1928
Tropidophis pardalis greenwayi Barbour and Shreve, 1936
Tropidophis pardalis barbouri Bailey, 1937
Tropidophis pardalis stejnegeri Grant, 1940
Tropidophis maculatus maculatus Bibron, 1840
Tropidophis maculatus haetianus Cope, 1879
Tropidophis maculatus jamaicensis Stull, 1928
Tropidophis maculatus pilsbryi Bailey, 1937
Tropidophis maculatus stulli Grant, 1940
Tropidophis nigriventris Bailey, 1937

We have examined 229 snakes representing the above forms; we wish to thank the following curators for their most generous loans of material, without which we would have been unable to undertake the present task: Mr. Charles M. Bogert, American Museum of Natural History (AMNH); Dr. James Boehlke and Mr. Edmund V. Malnate, Academy of Natural Sciences of Philadelphia (ANSP); Sr. Miguel L. Jaume García, Museo y Biblioteca de Zoología de la Habana (MBZH); Dr. Ernest E. Williams, Museum of Comparative Zoology (MCZ); Dr. Carlos G. Aguayo y de Castro and Dr. Isabel Pérez Farfante, Museo Poey (MP); Dr. Norman E. Hartweg, Museum of Zoology, University of Michigan (UMMZ); Mr. Oscar T. Owre and Mr. Dennis R. Paulson, University of Miami (UMRC); and Dr. Doris M. Cochran, United States National Museum (USNM). The collections from the Museo Poey and the Museo y Biblioteca de Zoología de la Habana are extremely interesting, pertinent, and valuable, and have heretofore not been available to American workers; we are especially grateful to Drs. Aguayo and Farfante,

Throughout the remainder of the text, the use of a trivial name only refers to specimens regarded as assigned to that named population and does not imply that relationships are quite as indicated in the list of recognized forms above. We have examined the following numbers of specimens from the West Indies: *androsi*, 10; *barbouri*, 15; *canus*, 20; *curtus*, 30; *greenwayi*, 2; *haetianus*, 11; *jamaicensis*, 11; *maculatus*, 17; *nigriventris*, 5; *pardalis*, 75; *pilsbryi*, 4; *stejnegeri*, 4; *stulli*, 2. In addition, there are four specimens from Cuba, one from the Cay Sal Bank, and 17 from the Bimini Islands, all of which require special comment. Insofar as we are concerned, all these named populations are valid, and no names will be regarded as synonyms; however, the degree of distinctness of the various forms varies greatly, and this criterion has been used to differentiate both subspecies and species in the present paper.

The following data have been taken on each specimen, as far as practicable; a few individual snakes have been so long in preservative that the details of pattern are faded and poorly shown, and a few others were probably preserved in strong alcohols and consequently are now almost worthless for study, but the majority of snakes have been completely useful. Pertinent data on all populations are given in Table I.

1) sex — since all males of this complex possess a pair of small spurs at the vent, distinguishing them from females is comparatively easy. Occasionally these spurs are small and partially retracted; in all dubious specimens dissection of the hemipenes was made.
2) total length, in millimeters
3) length of tail, in millimeters
4) number of ventral scales — counted in the manner proposed by Dowling (1951)
5) number of unpaired subcaudal scales, including terminal spine
6) number of supra- and infralabials
7) number of pre- and postoculars
8) number of scale rows around body behind head, at mid-body, and anterior to vent

9) presence or absence of contact between the parietal plates

10) number of longitudinal rows of body blotches, counted around body at midbody; this includes blotches on the venter

11) presence or absence of a pair of light occipital spots, easily distinguished from the dark dorsal ground color

12) color of the tip of the tail — either dark (including any coloration from tawny to olive to black) or light (undifferentiated from the remainder of the pale dorsal ground color or distinctly lighter than the dorsal ground color, probably yellow in life).

13) number of blotches, on right and left sides, in the two paramedian dorsal rows of blotches, counted from the first dark blotches behind the head to those just anterior to the vent

14) number of blotches on the dorsum of the tail; this count is subject to extreme variation since the caudal blotches may be paired, either regularly or irregularly, fused into dorsal saddles, alternating, or extremely reduced in extent.

15) keeling of dorsal scales — checked on dorsal rows of scales, especially above vent

Stull's grouping

Miss Stull (*op. cit.*:3-4) divided the forms of *Tropidophis* into two major groups, as noted above. The basis for this division was the character of the dorsal scales and the type of hemipenis, either bi- or quadrifurcate. The members of the *pardalis* group were represented as having the dorsal scales always more or less keeled ("varying from strong keeling even in young specimens . . . to weak keeling only in the most dorsal rows of full grown adults": Stull, *loc. cit.*), whereas the *maculatus* group was considered as having smooth scales. This difference appears not to exist when large series of specimens are considered. First, of 62 specimens of *pardalis* examined, 60 have the dorsal scales completely *smooth*, and only two have any indication of dorsal keeling; this is in definite contrast to Stull's statement as quoted above. Secondly, of 19 *maculatus*, eleven have distinct dorsal keels, and eight have these scales smooth; thus the basic character of smooth versus keeled scales as a primary character in distinguishing the "*pardalis*" from the "*maculatus*" group is useless, since the taxa from which the group names have been

taken are variable in this particular character, and Stull's original diagnoses of the groups is based upon inadequate data and material. That the situation reported here for the forms *pardalis* and *maculatus* is not unusual is shown by the fact that, if more than only a very few specimens of a taxon are available, both smooth and keeled dorsals are demonstrable in the material. In *jamaicensis* all specimens (ten) on which carination was determinable had smooth dorsals; this is the largest number of specimens representing a single taxon in which only one type of dorsal (keeled or smooth) occurs with consistency throughout the sample. Occasionally, even in small samples both types of scales are demonstrated; of four *pilsbryi*, three have the dorsals keeled and one has them smooth.

The carination of dorsals thus appears to be an invalid criterion in these boids; however, there are *tendencies* within populations toward either a preponderance of keeled or smooth dorsals. Thus the vast majority of *pardalis* have smooth scales (97%), most *curtus* have keeled scales (90%), most *haetianus* have smooth scales (91%), etc. The carination apparently does not depend upon either sex or ontogenetic changes; both males and females, and adults and young, appear to be indiscriminately keeled or smooth, without any obvious correlation. The two keeled *pardalis*, for example, are a juvenile female and an adult male, from two widely separated localities. To ascertain whether the dorsals are keeled or smooth is sometimes extremely difficult. In many instances the preservation and subsequent drying may have wrinkled the scales or curled them around the edges; some snakes have the dorsals much pitted or eroded (this is especially true of Bahaman snakes). All such dubious cases were left unrecorded, and it is probable that proportions in certain instances would be somewhat changed had we been able to determine this character on all specimens. Nonetheless, we feel certain that carination *per se* is not an all-or-none phenomenon in the *pardalis-maculatus* complex, and must be used with caution in diagnosing groups, with emphasis rather on tendencies within populations.

Stull's second character, that of the forking of the hemipenis, is apparently equally untenable. We have examined by dissection the hemipenes of all forms pertinent to the study. In addition, a few recently preserved specimens have the hemipenes extruded. In no cases have we seen quadrifurcate hemipenes. The appearance of double bifurcation is at times given by the bands of retractor muscle fibers, but in every case where this

superficial resemblance to a quadrifurcate hemipenis was seen
upon dissection, careful observation revealed that the hemipenis
was in actuality bifurcate. Extruded hemipenes (*nigriventris*,
barbouri, *jamaicensis*, *pardalis*) likewise are uniformly bifurcate
and show no evidence of the quadrifurcate condition. It is perti-
nent to point out here that Stull (*op. cit.*:11) cited only a single
male (MCZ 12445) of *maculatus* examined; we have studied this
snake. It lacks spurs, and the tail has been dissected; what were
apparently considered as being hemipenes are in reality the
paired scent glands, filled at present with much fragmented and
solidified musk. The snake is obviously a female; however, dis-
section of available *maculatus* males reveals that they do indeed
have a bifurcate hemipenis, as do all other known members of
the complex.

In summary, we are unable to differentiate between the "*par-
dalis*" and "*maculatus*" groups on the basis of the structure of
the hemipenes; all have a bifurcate rather than a quadrifurcate
structure. Stull's original statements concerning the two types
of hemipenes in the snakes involved have almost certainly led
other workers (Bailey, *op. cit.*:49) to attempt to relate more
recently described forms to one or the other group with possible
subsequent confusion. Both the characters used by Stull to dif-
ferentiate these two basic groups have been shown to be invalid,
at least insofar as the *pardalis-maculatus* complex is concerned.
We do not know what type of hemipenes occur in the South
American forms (*T. paucisquamis* appears to have a bifurcate
hemipenis), in *melanurus*, and in the *semicinctus* aggregate.

Size

We have no assurance, of course, that we have seen maximally
sized individuals of both sexes in all cases. This is especially true
of taxa which are represented by small series, and in two cases
(*stulli*, *greenwayi*) we have studied members of only one sex,
and in another (*pilsbryi*) have not seen adult females. Conse-
quently, comments on size are open to obvious criticism; however,
general trends can be noted and statements appropriately made.

The largest size among males is reached by *stejnegeri* (416
mm. in total length); the largest size among females is reached
by *haetianus* (712 mm.). In six forms (*pardalis*, *stejnegeri*,
jamaicensis, *canus*, *curtus*, *barbouri*), males reach a larger size
than females; of these, *stejnegeri* is represented by three females
and one male. In two forms (*maculatus*, *haetianus*), females

reach a larger size than males. In two forms (*androsi, nigriventris*), both sexes reach an equal size.

By ranking the largest individual of each sex of each form, a tentative index of overall size relative to the other members of the complex can be reached; since inadequate data are at hand for *pilsbryi, stulli* and *nigriventris*, these taxa are not included. From large to small, the forms may be thus arranged: *haetianus, stejnegeri,* and *canus; maculatus* and *greenwayi, jamaicensis, barbouri, curtus* and *androsi,* and *pardalis.* Of the three forms which are poorly represented, *pilsbryi* appears to be small, *stulli* moderate, and *nigriventris* large.

The tail length/total length ratio has been computed for all specimens; there is little or no sexual dimorphism in this character, and ratios for both sexes have been combined. In the complex, this ratio (X 100) varies from 9.4 to 16.5, in individual specimens. Averages for taxa vary between 10.7 and 13.7. Ranking the taxa from relatively short to relatively long tail yields the following series: *canus, jamaicensis, stejnegeri, stulli, greenwayi, maculatus, pilsbryi, barbouri, pardalis* (Cuba), *androsi, nigriventris, haetianus, curtus, pardalis* (Isla de Pinos), and Bimini snakes with the highest ratio. Comments on the significance of these ratios will be made at appropriate places later in this paper.

Scalation

The number of ventrals, subcaudals, pre- and post-oculars, supra- and infralabials, scale rows, and presence or absence of parietal contact have been variously used by workers to define and differentiate the populations in the *pardalis-maculatus* complex. The presence or absence of keels on the dorsal scales has already been partially commented on, but will be discussed further below.

The number of ventrals varies between a low of 140 (Cuban *pardalis*) and a high of 208 (*maculatus*). Ranked by the average number of ventrals (both sexes included), the populations can be thus arranged in a series from low to high average number of ventrals: *pardalis* (Cuba), *pardalis* (Isla de Pinos), *curtus,* Bimini snakes, *nigriventris, greenwayi, barbouri, androsi, stulli, pilsbryi, canus* and *jamaicensis, haetianus, stejnegeri, maculatus.*

The number of subcaudals in the complex varies from a low of 22 (*barbouri*) to a high of 41 (*maculatus*). The lowest average number of subcaudals occurs in *nigriventris* (25.5), with both populations of *pardalis* and that of *barbouri* slightly higher (28.2

to 29.9). The highest average number of subcaudals occurs in *hactianus* (37.0), with *maculatus* only slightly lower (36.3). The remaining taxa are intermediate between these extremes.

The number of preoculars is typically 1/1 in the entire assemblage of forms. Counts of 2/1 and 2/2 occur rarely, and all large lots of material invariably show a few individuals with these abnormal counts (three out of ten *androsi*, two out of 15 *barbouri*, one out of 20 *canus*, two out of 67 *pardalis*, etc.). The number of postoculars is likewise variable; here however, there seems to be a definite tendency within a population toward either 2/2 or 3/3 postocular scales. For example, Cuban *pardalis* usually have 2/2 postoculars (42 of 57 specimens), *maculatus* usually has 3/3 (15 of 17 specimens), *canus* usually has 3/3 (17 of 20 specimens). Counts of 2/3 are not common but do occur; abnormally, there is one *hactianus* with 3/5 and one boa from Bimini with 3/4. Of the specimens of *hactianus*, one (ANSP 10279) has a complete row of suboculars separating the eye from the supralabials, and another (USNM 75925) has a single subocular scale. Two specimens of *stulli* (MCZ 44871-72) both have a single subocular. These four snakes are the only specimens examined with subocular scales.

Supra- and infralabials are variable; the number of the former is usually 9/9 or 10/10, but occasional specimens have 8, 11, or 12 on one or both sides, and all combinations from 8 to 12 may occur. Infralabials likewise vary from 9/9 to 12/12, with an occasional 13 unilaterally. Neither supra- nor infralabials are useful, in our opinion, in defining or differentiating populations.

The number of scale rows at midbody is another character which varies within populations, and only tendencies can be pointed out. In any considerable series from a population, at least two counts occur, and sometimes three. In general, the forms may be said to be characterized by the following number of scale rows at midbody, although it must be remembered that there are exceptions in every case:

23 scale rows — *pardalis, canus, curtus, nigriventris*
25 scale rows — *maculatus, stulli*, Bimini, *androsi, barbouri, greenwayi*
27 scale rows — *stejnegeri, hactianus*

The populations of *jamaicensis* and *pilsbryi* cannot be categorized; of four specimens of *pilsbryi*, each has a different midbody count — 23, 24, 25, 27. Probably this form belongs to the 25 scale-row group. Of nine *jamaicensis*, four have counts

of 25, three of 27, one of 26, and one of 29; this form probably belongs with the 27 scale-row group.

As far as parietal contact is concerned, as with all other scale characters, this one is also variable. When any sizable series is studied, usually some specimens will have the parietals in contact and others will not. The only major exception to this statement is that all 15 specimens of *barbouri* examined lack parietal contact. The general tendency is, however, for all members of the group to lack parietal contact; exceptions to this statement are Isla de Pinos *pardalis, haetianus,* and *greenwayi*. These three populations have more individuals with the parietals in contact than without contact; in fact, *greenwayi* was partially diagnosed (Barbour and Shreve, *op. cit.*:2) on this basis. However, as in other members of the group, the Bahaman forms *canus* and *curtus* show some individuals with the parietals in contact, and it is probable that when other specimens of *greenwayi* are collected some will show lack of contact between the parietals.

The use of carination of dorsal scales as a character in separating the "*pardalis*" and "*maculatus*" groups has been made previously, and attention was then drawn to the variability of this character within populations. Those taxa which show a tendency toward smooth scales include: *pardalis, jamaicensis, stulli, haetianus,* Bimini snakes, *greenwayi,* and *nigriventris;* whereas *maculatus, pilsbryi, stejnegeri, canus, curtus, androsi,* and *barbouri* have more individuals with keeled than with smooth scales. It should be kept in mind that these are tendencies only, and in any large series from the same general locality individuals may be found with keeled or smooth scales.

Pattern

All members of the *pardalis-maculatus* complex are distinguished from the other West Indian members of the genus by having a tan to brown dorsum with a series of many, more or less prominent, darker blotches from the occiput to the tail. A constant feature among the forms is the presence of paired blotches on the venter; these may be large and conspicuous as in *pardalis* (Fig. 1) and *nigriventris* (Fig. 2), or much restricted and almost absent as in *stulli* (Fig. 3). Including these two ventral rows, there are from six to twelve longitudinal rows of blotches or spots in the complex. Again, as with the other characters already treated, within populations the number of rows is not constant if large series are examined. The only major exception to this statement is that nine of the ten *androsi* examined

had 10 rows of blotches (one was indeterminate). The largest variation in number of rows is in the series of 17 specimens from Bimini; here, counts of 8, 9, 10, 11 and 12 rows were encountered, with 10 rows being the most frequent. The populations of *canus* and *maculatus* are also rather variable, the former having counts of 6, 7, 8, 9 (6 rows most frequent), and the latter 6, 8, and 10 (8 rows most frequent).

Basing our conclusions on the frequency of occurrence of number of rows in samples examined, we would categorize the following taxa by rows of blotches as follows:

6 rows — *pardalis* (Cuba), *canus*

8 rows — *pardalis* (Isla de Pinos), *maculatus, pilsbryi, stejnegeri, nigriventris*

10 rows — *stulli, jamaicensis, haetianus, curtus,* Bimini snakes, *androsi, barbouri*

In the above summary, *greenwayi* is not included; the two specimens at hand have 8 and 10 rows of blotches. The much faded *stulli* was diagnosed by Grant (1940:8) as having only two rows of dorsal spots; this is true anteriorly, but posteriorly the complete complement of 10 rows of blotches can be determined.

The distinctness of the blotches varies both between and within populations. In some forms (*maculatus,* Fig. 4) the blotches stand out boldly against a much paler ground color which in general lacks accessory interblotch dark pigment. In others, such as *pardalis* and some of the Bahaman populations, the blotches are less distinct. Coupled with this is the prevalence in the Bahaman forms (*canus, curtus, androsi, barbouri,* but not necessarily *greenwayi* of which no juveniles and only two adult males are known) of a radical ontogenetic change in pattern. In these forms, the juveniles are heavily and profusely spotted with dark gray to brown blotches on a lighter ground color (Fig. 5); these spots become increasingly less prominent with age and adults of both sexes are often but faintly spotted, the spots being much restricted and small (Fig. 6), or are completely unicolor tan to brown with no indication of spotting present. Such ontogenetic change does not occur in any of the other forms of which juveniles are known (*pardalis, maculatus, pilsbryi, haetianus*); in these forms the adult and juvenile patterns are identical.

The number of blotches in the paramedian longitudinal rows range in the complex from a low count of 25 (Cuban *pardalis*)

to a high of 90 (Bimini). In no instance can two forms be separated on the basis of number of blotches, although the size and extent of the blotches are often diagnostic. For example, the three Cuban forms (*pardalis, maculatus, nigriventris*) have blotch counts which overlap: 25-42 in *pardalis*, 33-54 in *maculatus*, 37-46 in *nigriventris*. However, inspection of a specimen of each of these snakes leaves no doubt as to which taxon it represents. In *pardalis* the blotches are large and dark, closely approximated, and relatively not prominent; in *maculatus*, the blotches are medium sized and very dark against a light ground color, and in *nigriventris* the blotches are small, appear to be more numerous and somewhat more crowded together and are not prominent, much as in *pardalis*.

The two ventral rows of blotches are usually far more prominent posteriorly than anteriorly; the extreme of this condition is shown by *stulli* where there is only the faintest indication of ventral spotting posteriorly, and the belly is almost immaculate anteriorly. The most prominent ventral blotches are in *pardalis* and *nigriventris*: in the latter the blotches may be so large as to be confluent, producing an almost black belly in some specimens.

Stull (*op. cit.*) and later Bailey (*op. cit.*) used the color of the tip of the tail as a feature to differentiate the various forms of the *pardalis* complex in the Bahamas. In general, the Bahaman populations have pale tails or tails which are unicolor with the dorsal ground color while they are young, and the dorsal surface of the tail becomes increasingly dark with age, in some instances olive green and in others dark brown to black. Often only the dorsal surface is affected, but in some individuals the entire distal portion of the tail may be involved. We have checked the tail color on all specimens, and the following remarks are based on the tail color of adults only (in juveniles the tail is almost uniformly pale or only as dark as the dorsal ground color). In only six populations is the tail more often light than dark: *pardalis* (both Cuba and the Isla de Pinos), *maculatus, jamaicensis, stulli, stejnegeri*, and *greenwayi*. Of *stulli* and *greenwayi* we have seen only two adults each and three adult *stejnegeri*, and consequently these data may be inaccurate. Of all adult *pardalis* examined (54), only two Cuban individuals have dark tails; of 14 adult *maculatus*, four have dark tails. The forms *haetianus, canus, curtus, androsi*, and *barbouri* more often have dark tail tips, but pale-tailed individuals of each of these populations have been examined. Too few *pilsbryi* and

nigriventris are known; two adult specimens of each were studied and in each case one has a dark and the other a light tail.

The presence of pale occipital spots has been used to distinguish various taxa in the group under consideration. In the Bahaman forms (*canus, curtus, androsi, barbouri, greenwayi*) no specimen of the 77 examined shows any indication of these spots. Neither do they appear in any specimen of *nigriventris, haetianus, stulli, jamaicensis,* or *maculatus.* In all specimens of *pilsbryi, stejnegeri,* and Isla de Pinos *pardalis,* the spots are present; they are a constant and bold pattern feature of *pilsbryi.* Only in Cuban *pardalis* are there individuals with and without occipital spots; 29 adults lack them and 18 adults possess them.

The other pattern feature which is restricted to the Bahaman group of forms is the presence of an anterior dark line extending from the posterior margin of the eye posteriorly along the body for a variable distance along the seventh or eighth scale row, and gradually becoming fragmented to form the second (counting the paramedian row as the first) of the dorsal rows of longitudinal spots. This longitudinal line is apparent in all the Bahaman forms except *greenwayi,* whose dorsal coloration and pattern is perhaps the most unorthodox of the entire assemblage of the *pardalis-maculatus* groups.

Proposed arrangement

It should be obvious from the foregoing comments that the present arrangement of trivial names needs serious revision. Characters which previously have been used to separate major groupings within this section of the genus have been demonstrated to be inadequate or invalid. Reliance upon carination of scales to distinguish between *species* is improper; in fact, almost all characters of squamation appear to be sufficiently variable as to cause confusion. Of all the characters used, we feel that coloration and pattern, combined with characters of scutellation (provided these are used with discretion and with the frank admission from the outset that we are dealing in many cases with trends and tendencies and not hard and fast categories), and overall size, appear to give the most satisfactory results for separating and combining the thirteen named forms into a more realistic and sound arrangement.

Analysis of species by geographic areas

We have arranged the various taxa by geographic areas, and discussion of the variation and relationships of the snakes in each of these areas follows.

The Bahamas. The five forms currently known from the Bahamas are as follows, with their respective ranges.

androsi — Andros Island and Mangrove Cay

barbouri — Long Island ; Eleuthera Island ; South Eleuthera Island; Warderick Wells Cay ; Cat Island

canus — Great Inagua Island

curtus — New Providence Island

greenwayi — Ambergris Cay, Caicos Island

In addition we have examined 17 specimens from the Bimini Islands (AMNH 73501-04, 73542, 73708, 75414-18, 75623, 76870-71, 68818; UMMZ 110869-70) and one (USNM 81536) from Doubleheaded Shot Cay which lies on the Cay Sal Bank between southern Florida and the northern coast of Cuba. Comments on these 18 specimens will be made below.

With the exception of *greenwayi,* the remaining four forms (plus the Bimini and Cay Sal specimens) are closely related and have many features in common. Among these features are : moderate size (males no larger than 408 mm., females 373), tail color usually dark in adults, complete absence of occipital spots, usually 10 rows of body blotches, parietal contact usually absent, dorsal scales usually keeled, postoculars more often 3/3, and scale rows either 23 or 25 at midbody. Ventrals range from 146 to 183, subcaudals from 22 to 37. In addition, these snakes have distinctly different juvenile and adult patterns as previously pointed out (Bailey *op. cit.*:48, had commented on the differences between juvenile and adult coloration and pattern), and have the longitudinal line along the anterior sides, a feature which is present in no other forms.

Of the four, *canus* can be distinguished from both *curtus* and *barbouri* by its higher (170-183) ventral count (149-157 in *curtus;* 154-165 in *barbouri*) and six rows of blotches; *androsi* differs from *curtus* in number of ventrals as well (157-173 in *androsi*). The number of scale rows at midbody, and ten rather than six rows of blotches distinguish *androsi* from *canus;* the former usually has 25, the latter always 23. The number of scale rows distinguishes *barbouri* from *curtus;* the former usually has 25, the latter usually 23. The forms *barbouri* and *androsi* are very close; although the number of ventrals overlap, the means are different (164.0 in *androsi,* 158.3 in *barbouri*). The tail is relatively shorter (10.7%) in *canus* than in any of the other Bahaman forms.

On the other hand, *greenwayi* is so distinctly different not only from the above Bahaman populations, but from all other members of this group (and from *melanurus* and the *semicinctus* assemblage as well), that its affinities are questionable. Whereas the other Bahaman snakes are typically pale tan with rather restricted dorsal blotches, both dorsally and ventrally, *greenwayi* is extremely dark. The blotches are very large and extensive, and with irregular edges; often adjacent spots in different rows are indiscriminately fused, and the brown interspaces are much stippled with black (Fig. 7). The ventral rows of blotches extend to the throat. The head itself is stippled black and white, giving a salt-and-pepper effect. There is no indication of the anterior lateral longitudinal line which is so characteristic of the other Bahaman snakes. The number of ventrals (157-158) falls within the range of *barbouri*, just above the range of *curtus*, and much below the range of *canus*. The supposedly diagnostic feature of absence of parietal contact may not necessarily be valid, since this character appears in, of the other Bahaman forms, at least *canus* and *curtus*. The smooth dorsal scales of *greenwayi* differ from the usually keeled scales of *canus*, *curtus*, *androsi* and *barbouri;* each of these (except *androsi*) does however occasionally have smooth scaled individuals. In having 25 scale rows, *greenwayi* resembles *androsi* and *barbouri*, but differs from the typically 23 scale-rowed *canus* and *curtus*. The latter however does have some 25 scale-rowed individuals. In summary, we feel that *greenwayi* is sufficiently distinct in coloration and pattern that it should not be regarded as closely related to the other Bahaman *Tropidophis*, and consequently we regard it as a separate species.

The 17 snakes from the Bimini Islands are also remarkable. At the time of Stull's revision, apparently there were no *Tropidophis* known from these islands; insofar as we know, the report of Hecht and Walters (1955) was the first recording of this genus from Bimini. These authors gave an excellent description of the ontogenetic changes involved in the Bimini snakes, and called them only *T. pardalis;* they compared them with the other Bahaman snakes, but left the question of subspecific determination unanswered. Unfortunately, the situation is not any clearer at present, despite the acquisition of additional material. The Bimini snakes have ventral counts of 140 to 160 (mean 153.8), and are thus closely comparable to *curtus* (range 149-157, mean 151.8). Nine of the 17 are juveniles. However, both males and females apparently reach a larger size than

curtus; the largest male *curtus* is 330, the largest male Bimini snake is 359, whereas the largest female *curtus* is 310, and the largest Bimini female is 362, with an incomplete tail. Ratio of tail length/total length is approximately the same in the two groups. Both usually have dark tails, always lack occipital spots, usually have 10 rows of blotches, lack parietal contact, and have approximately the same range of subcaudals. They differ most strikingly in three characters: the Bimini snakes usually have smooth rather than keeled scales, usually have 3/3 rather than 2/2 postoculars, and usually have 25 rather than 23 scale rows. None of these characteristics is definitive, however, and each population has characteristics of the other.

The herpetofauna of the Bimini Islands has been discussed by Oliver (1948); the amphibians include *Hyla septentrionalis* and *Eleutherodactylus ricordi planirostris* (both of which are rather widely distributed in the West Indies and Florida), and the reptiles are: *Sphaerodactylus notatus* (which is also widely dispersed), *Anolis carolinensis lerneri*, *A. distichus biminiensis*, *A. angusticeps chickcharneyi*, and *A. sagrei ordinatus*. Three of the anoles (*lerneri, biminiensis, chickcharneyi*) are restricted to the Biminis, whereas *ordinatus* is more widely distributed (Turk's Island to New Providence, Barbour, 1937:126). Of the four anoles, three (*angusticeps, carolinensis, sagrei*) are Cuban in origin and affinities, and one (*distichus*) is Hispaniolan. From these remarks it is apparent that: 1) the Bimini herpetofauna is derived from two sources, Cuba and Hispaniola, and 2) at least in some forms differentiation into distinct subspecies has occurred on the Biminis. The boas of Bimini are related neither to the Cuban nor to the Hispaniolan *Tropidophis*, at least closely; their affinities are distinctly with the remainder of the Bahaman complex. It also appears that some differentiation from the remainder of the complex has also taken place, but that this has not progressed sufficiently far, at least in our opinion, to be nomenclatorially recognized.

The Bimini *Tropidophis* are most closely related to *curtus*. Bimini and New Providence, where *curtus* is known to occur, are separated by some 130 miles of ocean; lying between these two islands is the much larger Andros Island, which is inhabited by the distinctly different *androsi*. All these islands are part of the Great Bahama Bank. The significance of this peculiar distribution of *curtus* remains unknown; it is probable that *curtus*, as here delimited, represents two distinct entities which fortuitously are genetically very similar. In the absence of any

concrete differences between the two populations, we have no choice but to regard them both as *curtus.*

One other Bahaman specimen requires comment. This is a juvenile female (USNM 81536) from Doubleheaded Shot Cay, on the Cay Sal Bank. This specimen represents the westernmost occurrence of the Bahaman group of snakes; the snake was originally reported (Cochran, 1934:46) as *T. pardalis pardalis,* but Bailey (*op. cit.*:50) later commented that it "has the typical coloration of Bahaman juveniles." Its 159 ventrals eliminate only *canus* from consideration; this number lies within the known range of ventrals of *curtus, androsi, barbouri,* and *greenwayi,* although we doubt strongly that it is related to the geographically remote and extremely distinct latter form. It is useless to speculate further upon the identification of this snake since there is nothing distinctive about it which will facilitate allocation. We wish merely to point out that there apparently is a population of *Tropidophis* with distinctly Bahaman (rather than Cuban) affinities on the Cay Sal Bank.

It may be wise to point out here that the name *Ungualia curta* Garman was based on a specimen reportedly from Cuba. Stull, with justification, regarded this provenance as "probably erroneous" (*op. cit.*:31). It will be shown later in this paper that there is a single specimen of the Bahaman group of snakes known from Cuba, and it is entirely possible that Garman's type was indeed Cuban in origin. Should this prove to be the case, it may well be that certain shifting in the nomenclature of this entire lot of snakes will be necessary.

In summary, we consider the Bahaman snakes to represent two species, not closely related to any of the other West Indian small boids, and not closely related to each other. One of these is composed of four recognizable subspecies, and the prior name for this group is *canus* Cope, 1868. In our opinion, the *Tropidophis* of the Bahamas should be designated as follows:

> *Tropidophis canus canus* Cope, 1868
> *Tropidophis canus curtus* Garman, 1887
> *Tropidophis canus androsi* Stull, 1927
> *Tropidophis canus barbouri* Bailey, 1937
> *Tropidophis greenwayi* Barbour and Shreve, 1936

Jamaica. Our comments on the Jamaican *Tropidophis* are hampered by the extreme paucity of specimens in American collections. We have seen only 16 specimens from the island representing the three known forms; remarkably, three of these are

erythristic, and are the only such individuals we have seen from anywhere in the West Indies. The three forms known from Jamaica are, with their distributions:

> jamaicensis — south slope
> stulli — Portland Point
> stejnegeri — north slope

Considering these snakes together, they share certain characteristics and have others which are quite distinctive. All are moderately sized snakes; stejnegeri reaches the largest size (416 in males, 352 in females). All have low tail/total length ratios (11.0-11.6). All have parietal contact and usually 3/3 postoculars, and the scale rows are either 25, 27, or 29. The number of rows of blotches is either 8 or 10, and a pale tail is more common than a dark one, although both jamaicensis and stejnegeri show the dark tail tip at times. Of the three, stejnegeri is most strikingly different. It alone has large occipital spots and has keeled dorsal scales; both stulli and jamaicensis lack spots and have smooth dorsals. The three forms are completely separable on the basis of number of ventrals: stulli has from 166 to 167 (166.5), jamaicensis from 169 to 178 (174.3), and stejnegeri from 184 to 187 (186.0).

The major problem with these three forms is their interrelationships. Stull (op. cit.:12) described jamaicensis as a race of maculatus; later Grant (1940:157) described stulli as a race of maculatus and stejnegeri as a race of pardalis. The early brief descriptions of Grant's new subspecies were later expanded (Grant, 1941b:119-122). In the light of our data, it is at once obvious that the association of the name stejnegeri with pardalis, and of jamaicensis and stulli with maculatus is incorrect. The supposition that pardalis has keeled scales and maculatus smooth scales is not correct, as has been mentioned earlier; in fact, the reverse is more or less true. Thus jamaicensis and stulli might more properly have been regarded as subspecies of pardalis, and stejnegeri of maculatus. Such a course has even less to recommend it than the former allocation. As far as we are concerned, the Jamaican snakes are not at all closely related to the Cuban pardalis and maculatus, and are far more closely related intra se than to these Cuban snakes. If relationship with Cuban snakes must be sought, then the Jamaican snakes as a group are more closely related to maculatus than pardalis, but this relationship is not close nor is it on a subspecific level. From pardalis, the Jamaican snakes differ in much larger size, relatively

shorter tails, usual absence of occipital spots (although *stejnegeri* and some Cuban and all Isla de Pinos *pardalis* have them), 8 or 10 rows of blotches (usually 6 in Cuban, 8 in Isla de Pinos *pardalis*), 3/3 rather than 2/2 postoculars, and 25, 27, or 29 scale rows (usually 23, occasionally 25, and never 27 or 29 in *pardalis*), and more ventrals. From *maculatus*, the Jamaican snakes differ in somewhat larger size and definitely more robust build, relatively shorter tail, smooth rather than keeled scales (although the scales are keeled in *stejnegeri* and smooth in some *maculatus*), and less ventrals and subcaudals. For reasons advanced later, we regard the Jamaican snakes as all belonging to one species, along with boas from other areas, and we withhold for the moment any use of trinomials. Certainly there is no question of the distinctness of the three Jamaican forms from one another.

Hispaniola. Only a single form, *haetianus*, has been recorded from Hispaniola (Stull, *op. cit.*:14-18; Cochran, 1941:325-329). In addition to occurring on the main island, this snake is known as well from Ile Tortue and Gonave Island. Cochran has discussed at some length the variation in coloration, pattern, and scutellation in *haetianus*, and little need be said concerning these matters here.

Comparing *haetianus* with the other West Indian snakes reveals that it is not closely related to the Bahaman *T. canus;* it differs in reaching a much larger size (*haetianus* is the largest member of the complex), usually has the parietals in contact, usually has the dorsals keeled (true as well only of *c. curtus* from Bimini, but occurring sporadically in the other Bahaman subspecies except *androsi*), and scale rows usually 27 (the type of *haetianus* is unique in having 29 scale rows), a count that has never been observed in any population of *T. canus.* In addition, *haetianus* lacks the change from juvenile to adult patterns and the longitudinal lateral dark line of the Bahaman snakes.

The association of *haetianus* with *maculatus* we regard as erroneous. The main difference is the presence of smooth scales in *haetianus* in contrast to keeled scales in *maculatus.* Also, *haetianus* reaches a much larger size, has a relatively longer tail, usually has a dark rather than light tail tip, has 10 rows of blotches (Fig. 8) rather than 8, usually has parietal contact, and has 27 rather than 25 scale rows. The number of ventrals is lower than in *maculatus*, but there is overlap between the two populations. The style of patterns is different in the two forms. In *maculatus* the blotches are prominent and dark on an almost

clear ground color; in *haetianus* the pattern is diffuse, obscure, and indistinct since the ground color is much stippled and dusky in the interspaces. The Hispaniolan snakes are, in addition, much more robust than *maculatus*.

The closest affinities of *haetianus* appear not to be with either of its two Cuban relatives, but rather with the snakes of Jamaica. Both *haetianus* and the Jamaican forms are relatively large and robust, both usually lack occipital spots, have 8 or 10 rows of blotches, usually are smooth scaled, have 3/3 postoculars and have 25, 27, or 29 scale rows. The basic patterns are very similar, although this pattern is much obliterated in *stulli*. Differences between them include relatively longer tail in *haetianus*, usually dark tail in *haetianus*, and usually parietal contact in *haetianus*. The range of ventrals in *haetianus* is comparable to that in the aberrant *stejnegeri* (180-192, mean 185.2 in the former; 184-187, mean 186.0 in the latter). The similarities between the Hispaniolan and Jamaican snakes outweigh, in our opinion, their differences; we are placing special emphasis on the similarity of patterns in the populations involved. For these reasons we regard the snakes of Jamaica and Hispaniola as belonging to one species, and the names may stand as:

> *Tropidophis haetianus haetianus* Cope, 1879
> *Tropidophis haetianus jamaicensis* Stull, 1928
> *Tropidophis haetianus stulli* Grant, 1940
> *Tropidophis haetianus stejnegeri* Grant, 1940

Cuba and the Isla de Pinos. More forms of the *pardalis-maculatus* complex occur in Cuba than on any other island of the West Indies; the situation has been made even more complicated by the fact that several of the forms (especially *maculatus*) have been poorly represented in American collections. Fortunately, this situation has been somewhat remedied, although inadequate material still makes certain problems unsolvable. The forms which have been known to occur on Cuba are:

> *pardalis* — widespread and on the Isla de Pinos
> *maculatus* — western Cuba and Isla de Pinos
> *pilsbryi* — central and eastern Cuba
> *nigriventris* — west central Cuba

Unaware of the possible diversity of Cuban *Tropidophis* at the time of her revision, Stull confused several specimens and forced

them into either *maculatus* or *pardalis*. This situation was partially remedied with Bailey's description of *pilsbryi* and *nigriventris*, but the picture was still not complete. We know that our contribution here is not the final word, but certain peculiariies and discrepancies can now be clarified.

The most widespread of the Cuban multispotted boas is *pardalis*, which occurs from one end of the island to the other (although it is still unknown from extreme eastern Oriente), and on the Isla de Pinos as well. We will discuss the Cuban and Isla de Pinos populations as two entities, since there are certain striking differences between them. In Cuba, *pardalis* is a moderately sized snake, the smallest of the entire complex; males reach at least a maximum size of 343 (tail incomplete), females 292. The tail is relatively short (12.9% in tail/total length ratio). The tail color in adults is usually pale (45 of 47 individuals), the occipital spots are usually absent in adults (30 of 48 snakes), but may be present in juveniles, blotch rows are usually 6 (8 rows occur in four of 55 specimens), there are few dorsal spots in the paramedian rows (25-42), the parietals usually do not touch, the scales are almost always smooth, there are usually 2/2 postoculars (42 of 57 specimens), there are usually 23 scale rows (although counts of 21, 22, 24 and 25 occur), and the number of ventrals is low (140-165). The heavily blotched venter will distinguish *pardalis* from all other West Indian *Tropidophis* except *nigriventris*. The low number of ventrals will separate *pardalis* at once from *maculatus* and *pilsbryi*, although the latter is represented by an individual with 160 ventrals, just below the highest count of *pardalis* (165). Comparison with *nigriventris* is made below.

The Isla de Pinos *pardalis* agree with the Cuban population in moderate size, having light tail tips, smooth dorsals, usually 23 scale rows at midbody, and comparable numbers of ventrals and subcaudals. They differ in always having occipital spots in both adults and juveniles, more often having 8 rather than 6 rows of blotches, more often having parietal contact, and more often having 3/3 postoculars. In combination these characters might justify the erection of a new taxon for the Isla de Pinos snakes. We are reluctant to do so because of the great overlapping of the characters; none is completely definitive, and all are matters of degree. In the following comparisons with other Cuban material, we will disregard the Isla de Pinos snakes, although well aware of their similarities and differences with reference to the Cuban populations.

Not included in the above discussion are a series of *pardalis* (ANSP 10251-56, 10280) with locality data "Cuba"; the first lot of these was collected by Felipe Poey, the single specimen apparently not by him. Of the series, two (ANSP 10254-55) have prominent occipital spots, and the former has 3/3 postoculars as well. It would not be surprising if these two snakes were actually from the Isla de Pinos; we know that Poey visited the Isla with Don Carlos de la Torre (Conde, 1958:221), and it is not impossible that these two snakes were collected there. Since there is doubt thus cast upon the entire lot, we have not utilized any data from this material in our computations and calculations.

Most closely related to *pardalis* is *nigriventris*. However, we do not regard this relationship as a subspecific one; both forms occur in the provinces of Las Villas and Camagüey. We have specimens which indicate that the two are precisely sympatric; in Las Villas, *pardalis* is known from Cumanayagua, Soledad, and Trinidad, and *nigriventris* from Trinidad as well. The only specimen of *pardalis* from Camagüey is from Paredón Grande, a key northeast of Cayo Romano, whereas *nigriventris* is known in Camagüey from the southeastern portion of the province, in the Martí-Camagüey city area. There are no specimens of *nigriventris* from Oriente where it may be expected, and we have seen only five specimens of *pardalis* from Oriente, all from San Germán in the central portion of the province. Specimens of *pardalis* from the Trinidad area have the highest ventral count of any examined, and Trinidad *nigriventris* have high counts as well; thus in southern Las Villas the two species are very close. It may be considered that the relationship is a subspecific one on this basis, but we are reluctant to assume so.

Based on a small sample of five snakes, *nigriventris* is seen to reach a larger size than *pardalis* (female *nigriventris* reach at least a size of 355 mm., and males 351 mm., both specimens in question having incomplete tails), but in all scale counts the two species are very close. Both lack occipital spots, lack parietal contact, have smooth dorsals, and have 23 scale rows. Of two adult *nigriventris*, the tail is dark in one and pale in the other; 2/2 postoculars occurs with more frequency (3 snakes) than 3/3 (2 specimens). Few Cuban *pardalis* have 8 rows of blotches; all *nigriventris* examined have 8 rows, although the two Las Villas specimens have the lowermost dorsal rows obsolete. The number of blotches in the paramedian rows varies between 25 and 42 in *pardalis,* and between 37 and 46 in *nigriventris*. Thus the latter

form has a few more blotches on the average than *pardalis*, but
the counts overlap greatly. The major differentiating feature of
the two snakes is the much smaller head of *nigriventris*; if speci-
mens of the two taxa are compared, the smaller head of *nigri-
ventris* is immediately apparent. The extent of the medial fusion
of the ventral blotches, giving an almost entirely black belly, is
too variable in *nigriventris* to be an absolute character; the two
Las Villas specimens (USNM 138512, 138510) have ventral
blotches which are less prominent and extensive than many *par-
dalis*.

Comparison of *nigriventris* with *maculatus* is almost unneces-
sary. The dark ground color and less conspicuous dorsal blotch-
ing of the former stand in direct contrast to the light ground
color and conspicuous pattern of the latter. The head of *macu-
latus* is not strikingly small, and *maculatus* usually has keeled
rather than smooth scales. The number of ventrals will also
separate the two populations (144-170 in *nigriventris*, 189-208
for *maculatus*).

The form *pilsbryi* was described by Bailey (*op. cit.*:42) on
the basis of three specimens, an adult male and two juvenile
females, all of which we have examined. These snakes are from
two widely separated areas — the Sierra de Trinidad in Las Vil-
las, and the Guantánamo Basin and Miranda in central and
eastern Oriente. The most obvious feature of *pilsbryi* is the
occurrence of one or a pair of light occipital spots which, in the
type, stand out boldly against the dark brown background. In
the original description, Bailey (*op. cit.*:43) commented on two
other Oriente specimens which he did not consider as being
pilsbryi; these are USNM 27455 and 12361. We have examined
both of these snakes; there is no reason to exclude USNM 12361
from *pilsbryi*. It is from "eastern Cuba" and thus within the
known range of the form, and, although the occipital spots are
rather faint and the ventral count is four scales lower than those
of the type and paratypes, it can very appropriately be con-
sidered *pilsbryi*. As for USNM 27455, we agree with Bailey that
this snake, also from "eastern Cuba," is definitely not *pilsbryi*,
nor is it *pardalis*, to which Stull (*op. cit.*:28) assigned it. It will
be discussed in detail below.

Aside from the presence of occipital spots (which condition
pilsbryi shares with some Cuban *pardalis*, but in which form the
spots are never so bold or prominent), *pilsbryi* differs from
pardalis in smaller size (maximum, a male, 212); usually 8,
occasionally 10, rows of blotches; keeled dorsals; 3/3 postoculars;

scale row counts of 23, 25, and 27 (*pardalis* usually has 23, but may have 25); and higher ventrals (140-165 in *pardalis*, 160-178 in *pilsbryi*). From *nigriventris*, *pilsbryi* differs in having prominent occipital spots, being smaller, having a relatively longer tail, having keeled scales, and a greater number of ventrals. Both snakes may have dark bellies with rather prominent blotches (Fig. 9), but this feature is more conspicuous in *nigriventris* than in *pilsbryi*.

The name *maculatus* has been applied to moderately sized, laterally compressed snakes from western and central Cuba. Cochran (1941:327) applied this name to USNM 27455, from "eastern Cuba," but this designation is not correct. There is in addition one *maculatus* (MCZ 12455) from the Isla de Pinos. As a group, the *maculatus* differ from all other Cuban snakes in their much higher ventral count (189-208); there is no overlap in this character with any other discovered Cuban form (see, however, the discussion below). Only *pilsbryi* has keeled dorsals as frequently as does *maculatus*; *nigriventris* and *pardalis* are usually smooth scaled. The coloration and pattern of *maculatus* sets it off as well from all other Cuban snakes, as has been pointed out previously, and little confusion should result in identifications. Comparisons of *maculatus* with the other Cuban multi-spotted *Tropidophis* has been made in the above paragraphs.

The problem with the Cuban snakes is not one of whether these four named forms are distinct; this is eminently so. The question is, rather, what is the relationship of these snakes to one another, and to the remainder of the West Indian small boas as well? As far as we are concerned, the four Cuban snakes merit specific, rather than any combination of subspecific status. Of the four, *pardalis* and *nigriventris* are related; *maculatus* and *pilsbryi* are likewise related. But the former pair is apparently sympatric (or possibly the range of *nigriventris* is surrounded by that of *pardalis?*), and the resemblances may well be superficial. The latter pair are widely separated geographically; that *pilsbryi* may be more common than now known is indicated by the statement of Alayo (1951 :108) that *Tropidophis* sp. with (translated) "a large white spot on either side of the neck" were taken at Santiago de Cuba. Some 250 kilometers separate the easternmost station of *maculatus* (Managua, Habana Province) from the westernmost station of *pilsbryi* (Mina Carlota, Las Villas). Although these two snakes show some resemblances to one another (both have 8 rows of blotches, lack parietal contact, have keeled dorsals, 3/3 postoculars), the much smaller

known adult size of *pilsbryi* as well as the extremely prominent occipital spots (a feature which is never demonstrated in *maculatus*) and the dark rather than light ground color, make it seem more satisfactory at present to regard these snakes as belonging to distinct species.

As far as extra-Cuban relatives of each of the four Cuban populations is concerned, we feel that none has a close relative elsewhere. Certainly the formerly current tendency to call the Bahaman snakes all races of *pardalis* is extremely misleading; no two snakes could be more different than *pardalis* and *androsi*, for example. None of the Jamaican or Hispaniolan snakes is related so closely to *pardalis* as is *nigriventris*. The only non-Cuban West Indian *Tropidophis* which has anything approaching the occipital spots of *pilsbryi* is the Jamaican *stejnegeri*, and close relationship between these two snakes is improbable. We have already commented on the distant possibility of close relationship between *maculatus* and *T. haetianus*, but this too has been discarded. Insofar as we are concerned, each of the named Cuban forms should stand as a separate species, as follows:

> *Tropidophis pardalis* Gundlach, 1840
> *Tropidophis maculatus* Bibron, 1840
> *Tropidophis pilsbryi* Bailey, 1937
> *Tropidophis nigriventris* Bailey, 1937

We take this radical action with full knowledge that additional material may prove relationships at present unguessed between these four snakes; we do not doubt that there are grounds for others to challenge our separating these four species from the remainder of the West Indian multispotted boids nomenclatorially. Of the four, the relationship of *T. pardalis* and *T. nigriventris* is the closest, and future collections may reveal that the two are subspecifically related.

There are four specimens of *Tropidophis* from Cuba which have caused endless confusion to ourselves and to other workers as well. These snakes are:

> AMNH 2946 — Nuevitas, Camagüey
> USNM 27455 — eastern Cuba
> MCZ 47896 — Guardalavaca, Banes, Oriente
> USNM 137084 — Soledad, Cienfuegos, Las Villas

Of these four, AMNH 2946 is extremely interesting. This snake was called *T. p. pardalis* by Stull (*op. cit.* :28), but it certainly is not this species. In coloration, scalation, and markings,

this snake belongs to the Bahaman assemblage, and is thus correctly assigned to *T. canus*. It is a young female, 195 mm. in total length, which possesses the adult pattern; the tail is pale, there is no parietal contact, the preoculars are 2/2, postoculars 3/3, the dorsals are keeled, there are 25 scale rows at midbody, 10 rows of blotches, and 48 and 51 blotches in the paramedian blotch rows on each side. The low number of ventrals eliminates only *T. c. canus* from further consideration; no other character or combination of characters will make it possible to assign this specimen to one of the three remaining subspecies of *T. canus*. An intriguing possibility is, of course, that this specimen represents true *Ungualia curta* Garman, originally described from Cuba. Geographically, certainly, one might expect a Bahaman species to occur in eastern, rather than western, Cuba. It is entirely possible that, with accumulation of additional *Tropidophis* from eastern Cuba, a population of *T. canus* will be discovered to occur in that area. Also Nuevitas is a seaport, and introduction of this single snake from New Province is not a remote possibility.

The remaining three snakes have had varied histories; only one (USNM 27455) is an old specimen. This snake was designated as *T. p. pardalis* by Stull (*op. cit.*:28), although she commented on the unusually high number of ventrals. Bailey (*op. cit.*:43) stated definitely that it is not *pilsbryi*. Cochran (1941:327) regarded it as *maculatus*. The two other specimens are more recently collected.

These three snakes (USNM 27455, MCZ 47896, USNM 137084) are very much alike and almost certainly represent the same form. Among them ventrals range from 178 to 191 (mean. 184.0), subcaudals 33 to 34 (33.5), two have dark tails and in the other the tail is light, occipital spots are absent in two and present in one, all have 10 rows of blotches, parietals are in contact in two and not in one, all have 3/3 postoculars, and scale rows are 25 in two and 26 in one. The tail/total length ratio is high (13.0-13.2, mean 13.1). These snakes are obviously closely related to *T. haetianus*, and may well represent a Cuban subspecies of the Jamaican and Hispaniolan snake in central and eastern Cuba. They are closest to *T. h. haetianus* in all characters, but are much smaller (largest female 244, largest *h. haetianus* 712), have keeled rather than smooth dorsals, and have 25 rather than 27 scale rows. The general style of pattern and pigmentation is comparable. As a group they have little in common with *pardalis* or *maculatus*, and likewise do not appear

related to *pilsbryi* or *nigriventris*. We can merely point out at present that a representative of *T. haetianus* does occur in central and eastern Cuba; subspecific allocation must await further material, although for the moment these snakes seem most closely related to *T. h. haetianus*.

Discussion

The transition from the past concept of three species of *Tropidophis* in the West Indies (*pardalis, maculatus, nigriventris*), two of which were regarded as polytypic, to seven full species, five of which are monotypic, has been based on examination of considerably more material than has been available heretofore to other workers. Although the arrangement proposed here may seem a radical departure from the old system, we feel that it better expresses the relationships of the populations of these snakes in the West Indies. Taxonomy has a twofold duty, to express both differences and likenesses, and our arrangement tries to keep to a middle road in this regard. There has been a tendency in recent years to group together allopatric forms without due regard for factors other than their allopatry. In several instances, accumulation of additional material has shown such groupings to represent a complex of species, rather than an assemblage of subspecies.

It is not surprising that Cuba, the largest of the West Indian Islands, has the greatest variety of species of *Tropidophis*, not only in the *pardalis-maculatus* complex, but in the genus as a whole. As currently understood, the Cuban forms are: *T. pardalis, T. maculatus, T. pilsbryi, T. nigriventris*, possibly *T. canus* and certainly a representative of *T. haetianus*, and in addition *T. melanurus melanurus, T. semicinctus, T. wrighti*, and *T. feicki*. Both Jamaica and Hispaniola have representatives of *T. haetianus*, and the Bahamas are occupied by *T. canus*, with *T. greenwayi* on the outlying Caicos Bank. The genus is absent from Puerto Rico and the Lesser Antilles; it does occur in South America (*T. paucisquamis, T. taczanowskyi*), on the Cayman Islands (*T. melanurus caymanensis, T. melanurus parkeri*), and Navassa Island (*T. bucculentus*).

We have examined one specimen of *taczanowskyi* and one of *T. paucisquamis*. Stull (*op. cit.*:4) postulated origin of the West Indian forms from both of these South American snakes; she had not examined hemipenes of either of them. The single

T. taczanowskyi (USNM 119009) is a female; the *T. pauci-squamis* (AMNH 72426) is a new-born male and apparently has bifurcate hemipenes. Of the two, *paucisquamis* has 21 scale rows and smooth dorsals, whereas *taczanowskyi* has 23 scale rows and prominently keeled dorsals — in fact, far more prominently keeled than those of any of the *pardalis-maculatus* group from the West Indies. Judging from Stull's descriptions and our examination, both of these species seem closer to the assemblage of forms under discussion than they do to either the *melanurus-bucculentus* group or the *semicinctus* group. Of the two, *taczanowskyi* appears more closely related, and *paucisquamis* more distantly related, to the assemblage. The dorsum of *taczanowskyi* is pale tan with three faintly indicated rows of blotches. The ventral blotches are large and black, and very prominent. These blotches are quite comparable to the ventral blotches of *T. pardalis*. The low ventral count (150), pale tail, and 23 scale rows all seem to ally *taczanowskyi*, in addition, to *pardalis*. However, the very distinctly keeled scales and the much faded dorsal pattern (with apparently three faint rows of blotches dorsally) serve to distinguish the two forms at once.

The single *T. paucisquamis* is so small that little can be determined about it. The blotches are apparently in eight longitudinal rows, and the entire tail is pale yellow dorsally and has four bold black blotches ventrally; this scheme of coloration and pattern is like that of none of the West Indian snakes. The venter has two longitudinal rows of irregular black blotches, reminiscent of, but not exactly like, those of *pardalis*. The dorsal pattern is peculiar, having a distinctly pale middorsal band about six scales in width, its margins scalloped by the lateral dusky ground color and the paramedian blotch rows. All these factors, plus the low number of scale rows (21), seem to set off *T. paucisquamis* from consideration as being on any direct line of origin for any of the West Indian forms; its very different characteristics indicate that it and the West Indian snakes have had a long and isolated history. Certainly additional specimens of both *T. tacznawoskyi* and *T. paucisquamis* are badly needed for study.

If we assume that there has been an increase in number of scale rows within the genus, then, of the *pardalis-maculatus* complex, those species with the lower number of dorsal scale rows (*pardalis*, *canus*, and *nigriventris*) will be the more primitive, and that with the higher number of scale rows (*haetianus*) will be the more advanced, with the remaining species between. The

nature of the carination of the dorsal scales may not be profitably used since in all taxa of the group both keeled and unkeeled snakes occur; we think however that carinate dorsals are more primitive than smooth dorsals.

It is interesting to note that of the three species just mentioned as having a low number of scale rows, two (*pardalis, nigriventris*) occur on Cuba (Fig. 10), and the third (*canus*) may possibly be there. The close affinities of *nigriventris* and *pardalis* have already been commented upon. *T. canus* and its subspecies in the Bahamas may well have been derived from *pardalis* in eastern Cuba (where it may occur still), or the occurrence of *T. canus* in eastern Cuba may represent a re-invasion into that area from the Bahamas. The latter is not likely however, since the currents along the north coast of Cuba flow towards, rather than from, the Bahamas (Marrero, 1951:44). It is interesting to note also that *T. c. canus* almost regularly (19 of 20 specimens) has 23 scale rows; this subspecies occurs on Great Inagua Island, that Bahaman island closest to the Cuban mainland, with the exception of the Cay Sal Bank group of keys. Differentiation on the Bahamas has been relatively slight, involving differences in number of ventrals, keeling of dorsals, obsolescence of juvenile pattern, and size; *T. greenwayi* stands as a notable exception to this statement. This species may well be a *T. canus* derivative, isolated, as far as known, on the rather remote Caicos Bank, which is separated from the Inaguas to the southwest and from the Acklin-Crooked island mass by deep troughs. No *Tropidophis* are known from either the islands of the Little Bahama Bank to the north, or from the more eastern islands (Rum Cay, San Salvador, Crooked, Acklin, Mayaguana, or Little Inagua) with the exception of the islands and cays of the Caicos Bank, where *T. greenwayi* is presumed to occur. The extreme differences of this species bespeak a long isolation from the remainder of the members of the group.

T. maculatus, T. nigriventris, and *T. pilsbryi* have the basic distribution characteristics of other Cuban amphibians and reptiles which have had rather long independent histories due to isolation on islands when Cuba was either an archipelago or several isolated islands corresponding roughly to the modern mountain masses. Thus, *T. maculatus* probably arose from a *T. haetianus*-like ancestor in the area of the Sierra del Rosario-Sierra de los Organos, *T. nigriventris* in the Sierra de Trinidad, and *T. pilsbryi* in the Sierra Maestra. Each of these is more or

less still restricted to these areas, although *nigriventris* has apparently spread to the east into Camagüey, and *pilsbryi* has spread to the west into Las Villas.

T. haetianus with 25 and 27 (and occasionally 29) scale rows seems to be the most advanced member of the complex; on Jamaica it has differentiated into three forms, whereas on the much larger island of Hispaniola only one form is known. This may indicate either a much longer residence on Jamaica than on Hispaniola, or that the species has been overly "split" taxonomically on the former island and that several subspecies occur on Hispaniola which are at present not or poorly represented in Hispaniolan material. As far as we are concerned, Hispaniolan material shows no striking differences within itself; this is rather surprising considering the subspecific differentiation of such snake genera as *Leimadophis* on Hispaniola. We postulate that *T. haetianus* is a relatively recent arrival to Hispaniola. Its occurrence in eastern Cuba is somewhat puzzling, but the similarity of Cuban and Hispanolian material may well indicate that this species has arrived at both islands from Jamaica at about the same time, and that little subsequent differentiation has taken place. Of the three Jamaican subspecies, we feel that *haetianus* and the Cuban snakes can best be derived from the more generally patterned, usually smooth scaled *jamaicensis*, which has an intermediate number of ventrals.

Darlington (1957:510 *et seq.*) discussed at some length the zoogeography of the West Indies. He postulated a double origin of the West Indian fauna, partially derived through migration via Cuba, and partially via Jamaica. Both invasions were presumably from Central America. If such a double origin is true, and there is no reason for doubting it, then the species of *Tropidophis* may be categorized in the following way. We imagine that *pardalis* is the basic stock in Cuba from which were derived *nigriventris* by isolation in the old Sierra de Trinidad, and *T. canus* via invasion of the Bahamas from Cuba. Of these two derived forms, the separation of *canus* and *pardalis* has been the longer. The relationships of *T. greenwayi* remain uncertain; it may either represent a long isolated offshoot of *T. canus*, or of *T. pardalis*, or it may have had some completely unknown history. The basic continental stock for this group of forms is most likely *T. taczanowskyi*, for reasons mentioned above. In the series, the number of scale rows goes from the primitive condition of 23 rows (*taczanowskyi*, *pardalis*, *nigriventris*, *canus*, *curtus*) to 25 (*androsi*, *barbouri*, and *greenwayi*).

Invasion of the West Indies via Jamaica can be used to account for the distributional pattern of *T. haetianus,* with forms on Jamaica, Hispaniola, and Cuba. We suspect that *pilsbryi* and *maculatus* represent isolates from this basic stock, isolates which have had long independent histories in the Sierra Maestra and the Sierra de los Organos respectively. In this second group of species, the scale rows are 25 in the more primitive members (*stulli, maculatus, pilsbryi* (?), and Cuban *haetianus*) to 27 (occasionally 29) in the more advanced members (*jamaicensis, haetianus, stejnegeri*).

Specimens examined

Tropidophis canus androsi: **Bahamas:** Andros Island, 8 (AMNH 2925-27, 63112; USNM 49471-72, 49474, 64156); Mangrove Cay, Andros Island, 2 (AMNH 63113; UMMZ 103982).

T. canus barbouri. **Bahamas:** Long Island, Clarencetown, 6 (AMNH 77008-12; UMMZ 117024); Long Island, Simm's, 1 (UMRC 55.139); Warderick Wells Cay, Exuma Cays, 1 (AMNH 77013); South Eleuthera Island, 2 (USNM 120804-05); Eleuthera Island, 3 (AMNH 73836-37; UMMZ 117278); Eleuthera Island, Hatchet Bay, 2 (AMNH 69178; UMMZ 99227).

T. canus canus. **Bahamas:** Great Inagua Island, 3 (AMNH 63335-37); Great Inagua Island, southwest point, 10 (AMNH 45839-47; UMMZ 117025); Matthew Town, Great Inagua Island, 1 (AMNH 45838); Inagua Island, 6 (USNM 26736, 7111 (5 specimens)).

T. canus curtus. **Bahamas:** New Providence, 19 (USNM 36594-95; MCZ 6241, 6491, 6969 (4 specimens), 6780, 6781 (2 specimens), 7089, 7090 (3 specimens); ANSP 10271-74); Nassau, New Providence, 7 (AMNH 2617, 7713; MCZ 8734-38); "British West Indies," 1 (ANSP 10278); no data, 3 (ANSP 10282-84); Bimini, 6 (AMNH 73501-04; UMMZ 110869-70); South Bimini, 8 (AMNH 73542, 73708, 75414-18, 75623); South Bimini, north side, 2 (AMNH 76870-71); South Bimini, west end, 1 (AMNH 68818).

T. canus subsp. **Bahamas:** Cay Sal Bank, Doubleheaded Shot Cay, 1 (USNM 81536); *Cuba,* Camagüey Prov., Nuevitas, 1 (AMNH 2946).

T. greenwayi. **Bahamas:** Ambergris Cay, Caicos Island, 2 (MCZ 42051-52).

T. maculatus. Cuba, Pinar del Río Prov., Guane, 1 (MCZ 10836); Pinar del Río, 1 (MP); Viñales, 1 (MP 179); Puerta

del Ancón, 1 (MP) ; Consolación del Sur, 1 (MP) ; La Deseade,
1 (MP) ; Habana Prov., Almendares, 1 (MP 186) ; La Habana,
3 (MP, MCZ 22901, USNM 56328) ; La Habana?, 1 (MP 59) ;
Botanical Gardens, La Habana, 2 (MCZ 7930-31) ; Bosque de la
Habana, La Habana, 1 (MP 286) ; near Río Quibús, Marianao, 1
(MBZH 26) ; Managua, 2 (MP 23) ; no locality other than Cuba,
1 (ANSP 10250) ; *Isla de Pinos*, no other locality, 1 (MCZ
12445).

T. pilsbryi. *Cuba*, Las Villas Prov., Mina Carlota, 1 (UMMZ
65043) ; Oriente, Cayo del Rey, near Miranda, 1 (ANSP 20822) ;
Guantánamo, 1 (MCZ 9884) ; "eastern Cuba," 1 (USNM 12361).

T. pardalis. *Cuba*, Pinar del Río Prov., Pedrera de Mendoza,
Mendoza, Guane, 1 (MBZH 62) ; 2 kilometers from Artemisa,
1 (MBZH 17) ; El Guamá, 1 (USNM 27392) ; San Diego de los
Baños, 1 (USNM 27849) ; La Deseade, 2 (MP) ; Herradura, 1
(MP 183) ; Habana Prov., Bosque de la Habana, La Labana, 8
(MBZH 59, 66; MP (6 specimens)) ; Cojímar, 1 (MBZH 19) ;
El Cotorro, 7 (AMNH 76541-47) ; La Habana, 3 (USNM 58715-
17) ; 9 kilometers southeast of San José de las Lajas, 2 (AMNH
77783, 76563) ; La Ceiba, Marianao, 2 (MP) ; Marianao, 1 (MP
111) ; Country Club, Marianao, 1 (MP) ; Río Quibús, Marianao, 1
(MP) ; Jaruco, 1 (MP) ; Escaleras de Jaruco, 1 (MP 299) ;
Baracoa, 1 (MP 306) ; Caimito, 2 (MP) ; Ceiba del Agua, 1
(MP) ; Matanzas Prov., Matanzas, 2 (MP 546; USNM 26360) ;
Abra de Yumurí, 1 (MP 319) ; Las Villas Prov., Soledad, 3
(AMNH 77784; USNM 134355; UMMZ 76109) ; La Sierra,
north of Vega Alta, 1 (USNM 75823) ; Cumanayagua, 1 (MP) ;
Trinidad, 2 (USNM 137085, 138511) ; Camagüey Prov., Pare-
dón Grande, 1 (MBZH) ; Oriente Prov., San Germán, 5 (MP
200 (3 specimens), 213 (2 specimens)) ; Cuba, no other locality,
10 (USNM 12418, 36804; UMRC 55.503; ANSP 10251-56,
10280) ; *Isla de Pinos*, no other locality, 8 (CM 1522-23, 1526,
1528-31, 284; east base, Sierra de las Casas, just west of Nueva
Gerona, 2 (AMNH 78605, 81000).

T. nigriventris. *Cuba:* Las Villas Prov., Trinidad, 1 (USNM
138512) ; 10 miles west of Trinidad, 1 (USNM 138510) ; Cama-
güey Prov., Martí, 1 (UMMZ 70887) ; Finca El Porvenir, Loma
de la Yagua, 24 kilometers southwest of Camagüey, 2 (AMNH
81182-83).

T. haetianus haetianus. *Haiti:* Port-au Prince, 1 (USNM
70459) ; Trou Forban, 1 (USNM 117279) ; *Republica Domini-
cana*, Puerto Plata, 1 (USNM 10275) ; San Francisco Mountains,
1 (USNM 35979) ; nr. Cape Samaná, 1 (USNM 55046) ;

Guarabo, 1 (USNM 66716); Paradis, 2 (USNM 64910); "eastern Santo Domingo," 1 (ANSP 10279); "Santo Domingo?", 2 (USNM 14838 (2 specimens)); Gonave Island, En Cafe, 1 (USNM 75925).

T. haetianus jamaicensis. Jamaica: Kingston, 1 (MCZ 44871-72); Long Mt., Kingston side, 1 (MCZ 59202); Malvern, 4 (MCZ 59203, 59205, 59207-08); Malvern, Santa Cruz Mountains, 1 (MCZ 55745); Mona, 3 (MCZ 59204, 59206, plus one untagged); "West Indies," no other locality, 1 (MCZ 6707).

T. haetianus stulli. Jamaica: Portland Point, 2 (MCZ 44871-72).

T. haetianus stejnegeri. Jamaica: Montego Bay, 3 (USNM 42878-80); Balaclava, 1 (USNM 73275).

T. haetianus subsp. *Cuba:* Las Villas Prov., Soledad, Cienfuegos, 1 (USNM 137084); Oriente Prov., Guardalavaca, Banes, 1 (MCZ 47896); "eastern Cuba," 1 (USNM 27455).

T. taczanowskyi. Peru: Loreto Prov., Fundo Sinchono, 1 (USNM 119009).

T. paucisquamis. Brazil: Boracea, São Paulo, 1 (AMNH 72426).

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TABLE 1
Data on sixteen populations of *Tropidophis* from the West Indies.

Form	N		Largest specimen (total length)		Longest tail	
	♂	♀	♂	♀	♂	♀
pardalis (Cuba)	23	24	343	292	44	45
pardalis (Isla de Pinos)	6	4	315	284	51	35
nigriventris	2	3	351	355	48	31
maculatus	8	9	375	394	48	47
pilsbryi	2	2	212	—	31	—
jamaicensis	3	7	383	340	45	38

Table I (Continued)

Form	N ♂	N ♀	Largest specimen (total length) ♂	Largest specimen (total length) ♀	Longest tail ♂	Longest tail ♀
stulli	2	0	318	—	35	---
stejnegeri	1	3	416	362	50	39
haetianus (Hispaniola)	3	8	400	712	56	76
haetianus (Cuba)	1	2	212	244	28	24
canus	8	12	408	373	45	40
curtus (New Providence)	12	18	330	310	47	39
curtus (Bimini)	6	11	359	362	49	52
androsi	7	3	320	317	47	37
barbouri	9	6	365	334	50	38
greenwayi	2	0	355	—	42	—

TABLE II

Data on sixteen populations of *Tropidophis* from the West Indies.

Form	T/T1 X100 (mean and extremes)	Tail color (adults) dark	Tail color (adults) light
pardalis (Cuba)	12.9 (10.5-16.5)	2	45
pardalis (Isla de Pinos)	13.6 (11.9-16.1)	0	7
nigriventris	13.1 (13.0-13.2)	1	1
maculatus	12.2 (11.1-13.3)	4	10
pilsbryi	12.3 (11.0-14.6)	1	1
jamaicensis	11.0 (10.0-12.9)	4	5
stulli	11.6 (11.0-12.2)	0	2
stejnegeri	11.5 (10.8-12.0)	1	2
haetianus (Hispaniola)	13.3 (12.3-15.1)	6	2
haetianus (Cuba)	13.1 (13.0-13.2)	2	1
canus	10.7 (9.4-12.1)	14	5
curtus (New Providence)	13.5 (12.1-15.2)	26	2
curtus (Bimini)	13.7 (11.6-14.9)	4	2
androsi	13.0 (11.6-14.7)	8	1
barbouri	12.6 (11.0-14.4)	7	4
greenwayi	11.9	0	2

TABLE III
Data on sixteen populations of *Tropidophis* from the
West Indies.

Form	Rows of blotches (incidence in ( ))	Dorsal spots	Occipital spots (adults) present	Occipital spots (adults) absent
pardalis (Cuba)	6(51) ; 8(4)	25-42	18	30
pardalis (Isla de Pinos)	6(4) ; 8(5)	31-41	8	0
nigriventris	8(5)	37-46	0	5
maculatus	6(1) ; 8(14) ; 10(1)	33-54	0	14
pilsbryi	8(3) ; 10(1)	38-50	2	0
jamaicensis	8(2) ; 10(6)	45-54	0	9
stulli	10(2)	44-50	0	2
stejnegeri	8(2) ; 10(1)	49-56	3	0
haetianus (Hispaniola)	8(5) ; 10(6)	45-57	0	11
haetianus (Cuba)	10(3)	45-51	1	2
canus	6(10) ; 7(1) ; 8(7) ; 9(1)	40-59	0	19
curtus (New Providence)	8(2) ; 10(22)	40-56	0	28
curtus (Bimini)	8(1) ; 9(2) ; 10(9) ; 11(2) ; 12(3)	40-90	0	8
androsi	10(9)	43-53	0	9
barbouri	8(5) ; 9(2) ; 10(6)	38-53	0	12
greenwayi	8(1) ; 10(1)	39-44	0	2

TABLE IV
Data on sixteen populations of *Tropidophis* from the
West Indies.

Form	Parietal contact present	Parietal contact absent	Dorsal scales keeled	Dorsal scales smooth
pardalis (Cuba)	15	42	2	50
pardalis (Isla de Pinos)	6	4	0	10
nigriventris	0	5	0	5
maculatus	6	10	11	8
pilsbryi	0	4	3	1
jamaicensis	2	8	0	10
stulli	0	2	0	2
stejnegeri	0	4	4	0
haetianus (Hispaniola)	10	1	1	10
haetianus (Cuba)	1	2	2	1
canus	6	14	12	2
curtus (New Providence)	4	26	27	3
curtus (Bimini)	2	15	5	12
androsi	0	9	8	0
barbouri	0	15	12	2
greenwayi	2	0	0	2

TABLE V
Data on sixteen populations of *Tropidophis* from the West Indies.

Form	Postoculars $\frac{2}{2}$	$\frac{2}{3}$	$\frac{3}{3}$	other	Scale rows 23	25	27	other
pardalis (Cuba)	42	7	8		39	14	0	21(1); 22(2); 24(2)
pardalis (Isla de Pinos)	4	1	5		6	4	0	
nigriventris	3	0	2		3	1	0	24(1)
maculatus	1	1	15		0	16	0	
pilsbryi	0	0	4		1	1	1	
jamaicensis	1	0	6		0	4	3	26(1); 29(1)
stulli	0	0	2		0	2	0	
stejnegeri	1	0	2		0	1	3	
haetianus (Hispaniola)	0	0	9	3/5 (1)	0	0	11	
haetianus (Cuba)	0	0	3		0	2	0	26(1)
canus	2	1	17		19	0	0	22(1)
curtus (New Providence)	14	6	10		17	12	0	24(1)
curtus (Bimini)	3	2	9	3/4 (1)	4	9	0	24(4)
androsi	3	0	7		1	7	0	24(2)
barbouri	2	6	7		6	8	0	24(1)
greenwayi	2	0	0		0	2	0	

TABLE VI
Data on sixteen populations of *Tropidophis* from the West Indies.

Form	Ventrals	Caudals
pardalis (Cuba)	147.1 (140-165)	28.2 (23-34)
pardalis (Isla de Pinos)	149.5 (147-155)	29.9 (28-32)
nigriventris	155.0 (144-170)	25.5 (25-26)*
maculatus	197.6 (189-208)	36.3 (24-41)
pilsbryi	167.0 (160-178)	30.5 (30-31)
jamaicensis	174.3 (169-178)	32.8 (30-36)
stulli	166.5 (166-167)	33.0 (32-34)
stejnegeri	186.0 (184-187)	32.3 (31-33)
haetianus (Hispaniola)	185.2 (180-192)	37.0 (33-39)
haetianus (Cuba)	184.0 (178-191)	33.5 (33-34)
canus	174.7 (178-191)	30.8 (29-35)
curtus (New Providence)	151.8 (149-157)	32.2 (29-37)
curtus (Bimini)	153.8 (146-160)	31.2 (29-36)
androsi	164.0 (157-173)	32.4 (30-36)
barbouri	158.3 (154-165)	29.9 (22-33)
greenwayi	157.5 (157-158)	30

*33 in male with incomplete tail.